



Fungi infecting woody plants: emerging frontiers

P.W. Crous^{1,2}, M.J. Wingfield²

Published on 18 May 2018

Trees in natural forests and those managed in plantations of either native or non-native species are increasingly threatened by fungal diseases (Roy et al. 2014, Wingfield et al. 2015, Ghelardini et al. 2017). Typically, the field of forest pathology focuses on this topic. But ironically, it often fails to consider trees outside the classical forestry system. For example, it is unusual for forest pathologists to study diseases of fruit trees, even though these trees originate from natural forests. And their disease threats are closely linked to pathogens that have evolved with the trees where they are native (Burgess & Wingfield 2016, Mehl et al. 2017). There is also increasing evidence that trees share pathogens with woody plants that are not considered to be trees. An example here would be pathogens of grapevines where there are numerous latent pathogens such as those in the *Botryosphaeriales* shared between these plants (Van Niekerk et al. 2004, Yang et al. 2017).

This dedicated volume was planned specifically to accommodate a suite of papers covering fungi that occur on trees but also to include woody plants not typically treated by tree pathologists. Broadly, our intention was to draw attention to the fact that there are many groups of fungi including important pathogens that occur on forest and fruit trees, but also on woody plants not usually considered by plant pathologists working on tree health problems. Nine papers have been included in this volume that treat a range of pathogen groups including ascomycetes, basidiomycetes and oomycetes. For many of these organisms, Koch's postulates have been tested and pathogenicity has been confirmed. For others, these tests have yet to be undertaken and some are most likely not pathogens.

The genus *Fusarium* includes many important plant pathogens or secondary invaders. These fungi have been included in the top 10 globally most important genera of plant pathogenic fungi, based on perceived scientific and economic importance (Dean et al. 2012). *Citrus* is one of the most important fruit crops worldwide, second only to apple. *Neocosmospora* (*Fusarium*) *solani* s.lat. is the causal organism of a disease known as dry rot of *Citrus*. In a survey to identify fungal pathogens associated with *Citrus* in Europe, several *Fusarium*-like isolates were obtained from diverse symptomatic tissues. A total of 11 species (six *Fusarium* spp. and five *Neocosmospora* spp.) were isolated from dry root rot, crown, trunk or twig canker or twig dieback. The isolates included three new *Fusarium* species

that are described in the paper by Sandoval-Denis et al. 2018). They include species in the newly described *F. citricola* species complex; and *F. siculi* that is in the *F. fujikuroi* species complex. Species of *Phaeoacremonium* are associated with diseases occurring in woody plant tissues. The best-known of these include Petri and esca diseases of grapevines (Crous et al. 1996, Mostert et al. 2006) and dieback and cankers on other fruit trees and woody plants (Gramaje et al. 2015). Several species of woody plants growing in the proximity of vineyards or fruit tree orchards have been shown to harbour species of *Phaeoacremonium*. In a survey of more than 29 different woody plants growing in close proximity to vineyards in South Africa, 31 species were identified, including 13 novel species (Spies et al. 2018).

The *Botryosphaeriaceae* includes a wide assemblage of fungi that are associated with dieback and canker diseases of woody plants including both economically important crops and native trees (Slippers & Wingfield 2007, Phillips et al. 2013, Yang et al. 2017). Species of *Eucalyptus* are amongst the most widely planted trees to sustain plantation forestry globally. There are many examples where these trees are seriously damaged by species of *Botryosphaeriaceae* including by diseases such as stem cankers, shoot and twig blight. Following an extensive survey of *Eucalyptus* and adjacent plants in six provinces of China, 12 species of *Botryosphaeriaceae* were identified, including six new species, of which the *Lasiodiplodia* species were the most aggressive in pathogenicity tests (Li et al. 2018).

The genus *Seiridium* includes several important plant pathogenic species, three (*S. cardinale*, *S. cupressi* and *S. unicorn*) of which are involved in the disease of *Cupressus* spp. known as cypress canker (Graniti 1998, Barnes et al. 2001). Based on a morphological and phylogenetic study, Bonthond et al. (2018) have re-evaluated the taxonomy of *Seiridium*. Both *S. cardinale* and *S. unicorn* are redescribed, with a reference strain designated for each. Authentic material of *S. cupressi* was re-examined, a lecto- and epitype designated and two new species described. This study resolves a longstanding confusion surrounding the taxonomy of *S. cupressi*, which is one of the most important pathogens of *Cupressus*, having a wide global distribution (Graniti 1998).

Species in the *Diaporthales* (*Sordariomycetes*) are responsible for several diseases of trees that can result in severe damage (Marin-Felix et al. 2017). The classification of *Diaporthales* has changed drastically in recent decades, largely due to the plasticity and variability in morphological characteristics that have been applied to their taxonomy. Based on a multigene phylogeny, Fan et al. (2018) have defined 25 families in *Diaporthales*. Four of these families are associated with canker and dieback of tree hosts are treated in this study. These include three new fami-

¹ Westerdijk Fungal Biodiversity Institute, P.O. Box 85167, 3508 AD Utrecht, The Netherlands;
corresponding author e-mail: p.crous@westerdijkinstitut.nl.

² Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, 0002, South Africa;
corresponding author e-mail: mike.wingfield@fabi.up.ac.za.

lies (*Diaporthostomataceae*, *Pseudomelanconidaceae*, *Synnemasporellaceae*), and one new genus, *Dendrostoma* (*Erythrogloeaceae*). The *Diaporthaceae* includes several genera (Senanayake et al. 2017), of which *Diaporthe* is well-known as the causal agent of many important plant diseases, including fruit rots, dieback and stem cankers (Gomes et al. 2013).

Diaporthe species are commonly found associated with major diseases of grapevines (Mostert et al. 2001). Several of these species remain unidentified and have in the past been treated as phylogenetic taxa (Van Niekerk et al. 2005). Very few studies have dealt with the distribution of *Diaporthe* spp. on grapevine in Europe and other countries from the Mediterranean basin. Guarnaccia et al. (2018) conducted surveys in European countries giving rise to 175 *Diaporthe* isolates. These included various well-known and four new species. Inoculation tests were conducted to define the relative importance of these fungi.

Diseases caused by species of *Ceratocystis* as recently defined in the *Ceratocystidaceae* by De Beer et al. (2014) include vascular wilts, cankers, as well as rot of various root crops (Roux & Wingfield 2009). In recent years, there has been a worrying increase in newly emerging tree diseases caused by *Ceratocystis* spp. (Ploetz et al. 2013, Tsopelas et al. 2017). In this volume, Barnes et al. (2018) describe a new disease that is rapidly assuming crisis status in Hawai'i and that has colloquially been termed Rapid 'ōhi'a death (ROD). The disease has resulted in the death of hundreds of thousands of native *Metrosideros polymorpha* trees on the Big Island of Hawai'i (Mortenson et al. 2016). The pathogen responsible for the wilt symptoms was tentatively identified as *C. fimbriata* s.lat., and the disease was referred to as Ceratocystis wilt (Keith et al. 2015). However, results of a morphological and phylogenetic study by Barnes et al. (2018) have shown that two new *Ceratocystis* species, *C. lukuohia* and *C. huliohia*, are associated with ROD. Morphology and interfertility tests support the delineation of these new species and pathogenicity tests have shown that both taxa are pathogens although their relative importance has yet to be determined. Attempts are currently underway to prevent the spread of these two pathogens to the other islands of Hawai'i, which are currently disease free.

The oomycete genus *Phytophthora* includes many species that have a hemibiotrophic or necrotrophic lifestyle as primary plant pathogens, although many aquatic *Phytophthora* species appear to be saprophytes and opportunistic necrotrophic pathogens (Erwin & Ribeiro 1996, Nechwatal et al. 2013). Several *Phytophthora* species have both soil- and airborne life-cycles, causing root and collar rot on agricultural crops, and foliage and shoot blights tree hosts. Globally, it has been estimated that up to 66 % of all fine root diseases and more than 90 % of all collar rots of woody plants are caused by *Phytophthora* species (Tsao 1990). In 1996, only 50 *Phytophthora* species had been described (Erwin & Ribeiro 1996). Importantly, more than 100 new *Phytophthora* species have been described in the past two decades (Burgess et al. 2018). The review by Jung et al. (2018) in this volume provides new insights into the history, distribution, symptomatology, disease dynamics and impact of the most important canker, decline and dieback diseases caused by soil- and airborne *Phytophthora* species in Europe, Australia and the Americas.

The rust fungus *Uromykladium tepperianum* has been reported on more than 100 species of *Acacia*, as well as on closely related plant genera. More significantly, it has also been introduced into countries as an important biological control agent to reduce the impact of invasive weeds, such as *Acacia saligna* in South Africa (Wood & Morris 2007). Based on a phylogenetic study, Doungsa-ard et al. (2018) revealed that *U. tepperianum* represents a species complex, and described the new species

U. morrisii to accommodate the biocontrol agent introduced into South Africa. The authors describe 16 new species based on host range, morphology and phylogenetic data. They also make the important point that additional species of *Uromykladium* are likely to be discovered when more taxa are examined incorporating DNA data together with their morphology and biology. Their findings also underpin some of the potential consequences of introducing biocontrol agents prior to resolving their taxonomy, and using contemporary molecular techniques that can reveal cryptic taxa.

Papers in this volume raise important issues relevant to the health of trees and other woody plants that might share common pathogens or groups of pathogens. The global movement of plants and plant products is clearly leading to often devastating introductions of new plant pathogens into areas where they were previously not present. In many cases, these pathogens are introduced in the asymptomatic tissues of plants traded for nursery purposes or even as fruit (Crous et al. 2015, 2016). There are huge numbers of these fungi and other microbes, mostly undescribed and often unculturable forming part of the microbiomes of plants as has recently been shown for *Eucalyptus* by Kemler et al. (2013). Detecting these organisms has relied on microscopy in the past but in future will lean increasingly heavily on molecular techniques for quarantine and screening (McTaggart et al. 2016, Guarnaccia et al. 2017). As illustrated in the papers included in this volume, there is considerable common ground between mycologists working on woody plants inclusive of those pertinent to forestry and fruit farming. In this regard, there is cause to promote closer collaboration between mycologists and plant pathologists with specific interests in horticulture and forestry.

REFERENCES

- Barnes I, Fourie A, Wingfield MJ, et al. 2018. New *Ceratocystis* species associated with rapid death of *Metrosideros polymorpha* in Hawai'i. *Persoonia* 40: 154–181.
- Barnes I, Roux J, Wingfield MJ, et al. 2001. Characterisation of *Seiridium* spp. associated with cypress canker based on β -tubulin and histone sequences. *Plant Disease* 85: 317–327.
- Bonthond G, Sandoval-Denis M, Groenewald JZ, et al. 2018. *Seiridium* (Sporocadaceae): an important genus of plant pathogenic fungi. *Persoonia* 40: 96–118.
- Burgess TI, Simamora AV, White D, et al. 2018. New species from *Phytophthora* Clade 6a: evidence for recent radiation. *Persoonia* 41: 1–17.
- Burgess TI, Wingfield MJ. 2016. Pathogens on the move: 100 year experiment with planted eucalypts. *BioScience* 67: 14–25.
- Crous PW, Gams W, Wingfield MJ, et al. 1996. *Phaeoacremonium* gen. nov. associated with wilt and decline diseases of woody hosts and human infections. *Mycologia* 88: 786–796.
- Crous PW, Groenewald JZ, Slippers B, et al. 2016. Global food and fibre security threatened by current inefficiencies in fungal identification. *Philosophical Transactions of the Royal Society B* 371: 20160024.
- Crous PW, Hawksworth DL, Wingfield MJ. 2015. Identifying and naming plant-pathogenic fungi: past, present, and future. *Annual Review of Phytopathology* 53: 246–267.
- De Beer ZW, Duong TA, Wingfield BD, et al. 2014. Redefining *Ceratocystis* and allied genera. *Studies in Mycology* 79: 187–219.
- Dean R, Van Kan JAL, Pretorius ZA, et al. 2012. The top 10 fungal pathogens in molecular plant pathology. *Molecular Plant Pathology* 13: 414–430.
- Doungsa-ard C, McTaggart AR, Geering ADW, et al. 2018. Diversity of gall-forming rusts (*Uromykladium*, *Pucciniales*) on *Acacia* in Australia. *Persoonia* 40: 221–238.
- Erwin DC, Ribeiro OK. 1996. *Phytophthora* diseases worldwide. APS Press, St. Paul, Minnesota.
- Fan XL, Bezerra JDP, Tian CM, et al. 2018. Families and genera of diarthalean fungi associated with canker and dieback of tree hosts. *Persoonia* 40: 119–134.
- Ghelardini L, Luchi N, Pecori F, et al. 2017. Ecology of invasive forest pathogens. *Biological Invasions* 19: 3183–3200.
- Gomes RR, Glienke C, Videira CIR, et al. 2013. *Diaporthe*: a genus of endophytic, saprobic and plant pathogenic fungi. *Persoonia* 31: 1–41.

- Gramaje D, Mostert L, Groenewald JZ, et al. 2015. Phaeoacremonium: From esca disease to phaeohyphomycosis. *Fungal Biology* 119: 759–783.
- Graniti A. 1998. Cypress canker: a pandemic in progress. *Annual Review of Phytopathology* 36: 91–114.
- Guarnaccia V, Groenewald JZ, Li H, et al. 2017. First report of *Phyllosticta citricarpa* and description of two new species, *P. paracapitalensis* and *P. paracitricarpa*, from citrus in Europe. *Studies in Mycology* 87: 161–185.
- Guarnaccia V, Groenewald JZ, Woodhall J, et al. 2018. Diaporthe diversity and pathogenicity revealed from a broad survey of grapevine diseases in Europe. *Persoonia* 40: 135–153.
- Jung T, Pérez-Sierra A, Durán A, et al. 2018. Canker and decline diseases caused by soil- and airborne *Phytophthora* species in forests and woodlands. *Persoonia* 40: 182–220.
- Keith L, Hughes RF, Sugiyama L, et al. 2015. First report of *Ceratocystis* wilt on 'ōhi'a. *Plant Disease* 99: 1276.
- Kemler M, Garnas J, Wingfield MJ, et al. 2013. Ion Torrent PGM as tool for fungal community analysis: A case study of endophytes in *Eucalyptus grandis* reveals high taxonomic diversity. *PLoS ONE* 8: e81718.
- Li GQ, Liu FF, Li JQ, et al. 2018. Botryosphaeriaceae from *Eucalyptus* plantations and adjacent plants in China. *Persoonia* 40: 63–95.
- Marin-Felix Y, Groenewald JZ, Cai L, et al. 2017. Genera of phytopathogenic fungi: GOPHY 1. *Studies in Mycology* 86: 99–216.
- McTaggart AR, Van der Nest MA, Steenkamp ET, et al. 2016. Fungal genomics challenges the dogma of name-based biosecurity. *PLoS Pathogens* 12: e1005475.
- Mehl JWM, Slippers B, Roux J, et al. 2017. Overlap of latent pathogens in the Botryosphaeriaceae on native and agricultural hosts. *Fungal Biology* 121: 405–419.
- Mortenson LA, Hughes RF, Friday JB, et al. 2016. Assessing spatial distribution, stand impacts and rate of *Ceratocystis fimbriata* induced 'ōhi'a (*Metrosideros polymorpha*) mortality in a tropical wet forest, Hawai'i Island, USA. *Forest Ecology and Management* 377: 83–92.
- Mostert L, Crous PW, Kang C-J, et al. 2001. Species of *Phomopsis* and a *Libertella* sp. occurring on grapevines with specific reference to South Africa: morphological, cultural, molecular and pathological characterization. *Mycologia* 93: 145–166.
- Mostert L, Groenewald JZ, Summerbell RC, et al. 2006. Taxonomy and pathology of *Togninia* (Diaporthales) and its *Phaeoacremonium* anamorphs. *Studies in Mycology* 54: 1–115.
- Nechwatal J, Bakonyi J, Cacciola SO, et al. 2013. The morphology, behaviour and molecular phylogeny of *Phytophthora* taxon *Salix* soil and its redesignation as *Phytophthora lacustris* sp. nov. *Plant Pathology* 62: 355–369.
- Phillips AJL, Alves A, Abdollahzadeh J, et al. 2013. The Botryosphaeriaceae: genera and species known from culture. *Studies in Mycology* 76: 51–167.
- Ploetz RC, Hulcr J, Wingfield MJ, et al. 2013. Destructive tree diseases associated with ambrosia and bark beetles: Black swan events in tree pathology. *Plant Disease* 97: 856–872.
- Roux J, Wingfield MJ. 2009. *Ceratocystis* species: emerging pathogens of non-native plantation *Eucalyptus* and *Acacia* species. *Southern Forests* 71: 115–120.
- Roy BA, Alexander HM, Davidson J, et al. 2014. Increasing forest loss worldwide from invasive pests requires new trade regulations. *Frontiers in Ecology and the Environment* 12: 457–465.
- Sandoval-Denis M, Guarnaccia V, Polizzi G, et al. 2018. Symptomatic Citrus trees reveal a new pathogenic lineage in *Fusarium* and two new *Neocosmospora* species. *Persoonia* 40: 1–25.
- Senanayake IC, Crous PW, Groenewald JZ, et al. 2017. Families of Diaporthales based on morphological and phylogenetic evidence. *Studies in Mycology* 86: 217–296.
- Slippers B, Wingfield MJ. 2007. Botryosphaeriaceae as endophytes and latent pathogens of woody plants: diversity, ecology and impact. *Fungal Biology Reviews* 21: 90–106.
- Spies CFJ, Moyo P, Halleen F, et al. 2018. *Phaeoacremonium* species diversity on woody hosts in the Western Cape Province of South Africa. *Persoonia* 40: 26–62.
- Tsao PH. 1990. Why many *Phytophthora* root rots and crown rots of tree and horticultural crops remain undetected. *Bulletin OEPP/EPPO Bulletin* 20: 11–17.
- Tsopelas P, Santini A, Wingfield MJ, et al. 2017. Canker stain: A lethal disease destroying iconic plane trees. *Plant Disease* 101: 645–658.
- Van Niekerk JM, Crous PW, Groenewald JZ, et al. 2004. DNA phylogeny and morphological characterization of *Botryosphaeria* species occurring on grapevines. *Mycologia* 96: 781–798.
- Van Niekerk JM, Groenewald JZ, Farr DF, et al. 2005. Reassessment of *Phomopsis* species on grapevines. *Australasian Plant Pathology* 34: 27–39.
- Wingfield MJ, Brouwerhoff EG, Wingfield BD, et al. 2015. Planted forest health: The need for a global strategy. *Science* 341: 832–836.
- Wood AR, Morris MJ. 2007. Impact of the gall-forming rust fungus *Uromycladium tepperianum* on the invasive tree *Acacia saligna* in South Africa: 15 years of monitoring. *Biological Control* 41: 68–77.
- Yang T, Groenewald JZ, Cheewangkoon R, et al. 2017. Families, genera, and species of Botryosphaeriales. *Fungal Biology* 121: 322–346.